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A SKULL AND MANDIBLE OF *GIRAFFOKERYX PUNJABIENSIS* PILGRIM

BY EDWIN H. COLBERT

The genus *Giraffokeryx* was founded by Dr. G. E. Pilgrim to designate a primitive Miocene giraffe from the lower Siwalik beds of northern India. Doctor Pilgrim, in a series of papers,[1] described *Giraffokeryx* on the basis of fragmental and scattered dentitions. Naturally, Pilgrim's knowledge of the genus was rather incomplete, and he was unable to formulate any opinions as to the structure of the skull or mandible.

An almost complete skull, found in the northern Punjab in 1922 by Mr. Barnum Brown of the American Museum, proves to be that of *Giraffokeryx*, and it exhibits such striking and unusual characters that a separate description of it has seemed necessary. This skull, together with numerous teeth and a lower jaw, gives us a very good comprehension of the genus which forms the subject of this paper. The drawings of the skull were made by John C. Germann, and the remaining ones were done by Margaret Matthew.

MATERIAL DESCRIBED

Only the material referred to in this description will here be listed. There are a great many specimens of *Giraffokeryx* in the American Museum collection, but since most of them are teeth, they will not be considered at this time. A subsequent paper, dealing with the American Museum Siwalik collection in detail, will contain a complete list of the *Giraffokeryx* material.

Amer. Mus. No. 19475.—A skull, complete back of the muzzle. The cheek teeth are preserved on both sides. The skull has been crushed to some extent. From the lower portion of the Middle Siwaliks, 1,000 feet below the Bhandar bone bed,[2] and one mile south of Nathot in the Punjab.

Amer. Mus. No. 19611.—Unassociated teeth. Lower Siwaliks, 200 feet above the level of Chinji Rest House and four miles west of that location, Punjab.

[1]Pilgrim, G. E. 1910. 'Notices of New Mammalian Genera and Species from the Tertiaries of India.' Rec. Geol. Surv. India, XL, Pt. 1, p. 69.
1911. 'The Fossil Giraffidae of India.' Mem. Geol. Surv. India, Pal. Indica, N.S., IV, No. 1, pp. 14–17; Pl. I, figs. 4, 5; Pl. II, figs. 1–16.

[2]The Bhandar bed was named by Pilgrim, from the village of Bhandar in the Jhelum district, Rawalpindi division of the northern Punjab. He considered this as an unfossiliferous horizon, but Brown, in 1922, opened a mixed quarry at this level, which yielded characteristic middle Siwalik fossils. The quarry was located one half mile north of Bhandar village. For the original designation of this horizon the reader is referred to: Pilgrim, G. E. 1913. 'Correlation of the Siwaliks with Mammal Horizons of Europe.' Rec. Geol. Surv. India, XLIII, Pt. 4, p. 277, Pl. XXVI.

Amer. Mus. No. 19472.—A right maxilla, with P^3-M^3. Lower portion of the middle Siwaliks, 1,200 feet below the Bhandar bone bed and one mile south of Nathot.

Amer. Mus. No. 19587.—The right ramus of a mandible, containing P_2-M_3. Lower Siwaliks, 200 feet above the level of Chinji Rest House and one and one half miles north of that place.

It may be seen from the above list that *Giraffokeryx punjabiensis* extends through the lower Siwaliks into the lower portions of the middle Siwaliks.

MORPHOLOGY OF THE SKULL

The skull of *Giraffokeryx* represents an animal of medium size and of peculiar form. As restored, it would measure some 500 millimeters in length, which though of fair size for the general run of ruminants, is small for the giraffes. The most striking features of this skull are the four horn cores, an anterior and a posterior pair, the former rising from the forward extremities of the frontals, and the latter from broad bases that rest partly on the frontals and partly on the parietals. The anterior horn cores spring from a common base, which is located above the first and second molars (perhaps it might be better to say that they are confluent at their bases), and they diverge laterally at an angle of approximately 105 degrees. These horn cores are directed posteriorly to a very slight extent, about 15 degrees. The posterior horns are widely separated basally. They arise directly back of the orbits, diverging laterally at an angle of approximately 80 degrees. Moreover, these horn cores are directed backwardly to an extent such that, as seen from the side, their median axes make angles of about 30 degrees with the perpendicular. These posterior horn cores are somewhat convex along their anterior borders, and at their bases, both on the anterior and the posterior edges, there are large rugose protuberances, as if in life there were basal accessory knobs or branches. Due to the great backward growth of these horn cores, their bases form a partial roof over the temporal fossae.

The true homologies of the "horn cores" of *Giraffokeryx* have been very perplexing, because since the skull is that of an old animal, the sutures are ankylosed to an extent that they have been largely obliterated. By a microscopic examination the naso-frontal suture has been established just anterior to the base of the front horn cores. The frontal-parietal suture can not be definitely located, but it would seem to cross the skull at a point about opposite the median portion of the posterior horn cores. The posterior horn cores of *Giraffokeryx* are therefore quite homologous with the similar structures in *Palaeotragus* and *Samotherium*, Asiatic Miocene and Pliocene giraffes, characterized by one pair of well

developed supraorbital horn cores. But the anterior pair in *Giraffokeryx* are without homologues among any of the Giraffidae, and must therefore be considered as neomorphic structures.

Of course there is a superficial resemblance between the skull of *Giraffokeryx* and that of the North American genus, *Syndyoceras*, because in both of these forms there are two pairs of horns, one pair being approximately supraorbital, while the other pair is placed above the muzzle. The resemblances between these genera are, however, attributable to functional analogies rather than to homologies, because while the

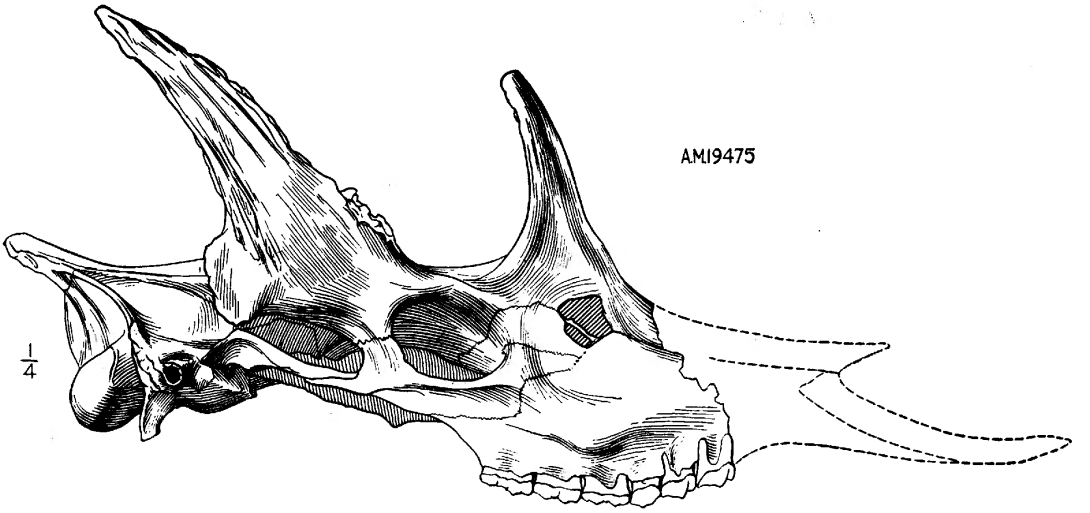

Fig. 1.—*Giraffokeryx punjabiensis* Pilgrim. Amer. Mus. No. 19475. Skull, right lateral view. Restored muzzle based on comparisons with *Palaeotragus* and *Okapia*. One-fourth natural size.

anterior horns are frontal upgrowths in *Giraffokeryx*, they are derived in *Syndyoceras* from the premaxillaries. In both genera the posterior horns are more nearly homologous, being frontal in *Syndyoceras*, and *fronto-parietal* in *Giraffokeryx*. Otherwise the skulls and dentitions show the taxonomic separateness that would be expected in these genera, for the Siwalik form belongs of course to the Giraffidae, and the North American genus is a member of the Protoceratidae, families that are related in kind, but which are nevertheless quite distinct from each other. *Synthetoceras*, recently described by Stirton, shows an accentuation of the *Syndyoceras* type of skull, and these two genera are closely related to each other.[1]

[1]Barbour, E. H. 1905. 'Notice of a New Fossil Mammal from Sioux County, Nebraska.' Neb. Geol. Surv., II, Pl. 3, four pages, one plate. (*Syndyoceras cooki.*)
Stirton, R. A. 1932. 'A New Genus of Artiodactyla from the Clarendon Lower Pliocene of Texas.' Univ. of California Publ., Bull. Dept. Geol. Sci., XXI, No. 6, pp. 148–149. (*Synthetoceras tricornatus.*)

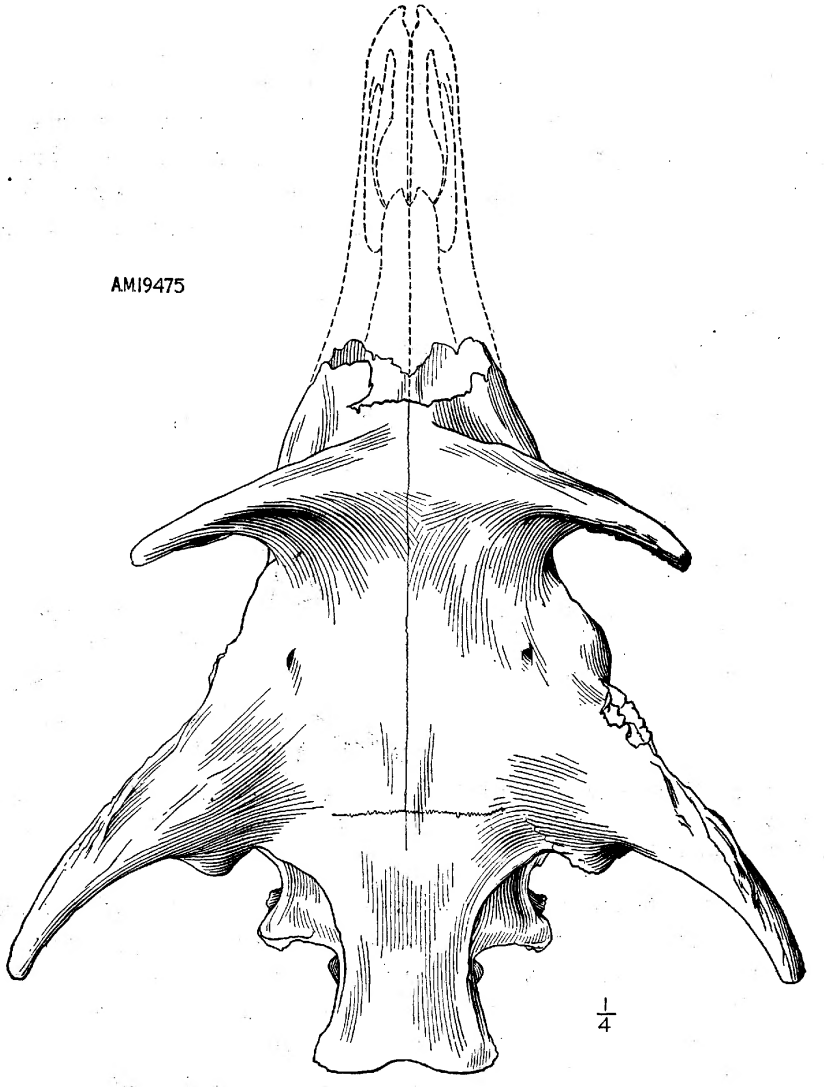

Fig. 2.—*Giraffokeryx punjabiensis* Pilgrim. Amer. Mus. No. 19475. Skull, dorsal view. Muzzle restored. One-fourth natural size.

Lankester,[1] in a series of papers, has demonstrated how in the modern okapi and giraffe, the "horns," or the *ossicones* as Lankester defined them, are developed in the skin as separated elements, becoming united with the skull as the animal approaches maturity. In the okapi, a persistent primitive form, having, like *Palaeotragus* and *Samotherium*, one pair of supraorbital horns, the ossicone coalesces with the frontal bone, and in the adult animal is firmly attached to that element. On the other hand, the ossicone in the foetal or newly born giraffe develops first above the parietal bone, but in consequence of growth factors it spreads anteriorly, so that in the adult it becomes attached to both the parietal and the frontal bones.

A growth process similar to that of the recent forms must have marked the development of the horns in *Giraffokeryx*. Indeed, the overlap of the base of each horn core on the roof of the skull is a striking character in this genus. Thus we may visualize small ossicones developing in the skin of the young *Giraffokeryx*, one pair above the anterior border of the frontals, and another pair over the back of the frontals. At maturity the front pair became attached to the frontal bones, but the posterior ossicones spread into long, elliptical bases that overlapped both the frontals and the parietals.

The nasals terminate posteriorly at the base of the front horn cores. The frontals are very wide, and extraordinarily flat, and behind them the parietals narrow rapidly and then flare out again to form the lambdoidal crest. The great constriction of the parietals in *Giraffokeryx* is an indication of the small size of the brain. The parietals dip down somewhat just behind the frontals, reaching the lowest point above the paroccipital processes, and then they rise again to the lambdoidal crest, which projects far behind the occipital condyles. There are supraorbital foramina piercing the frontals.

As seen from the side, the skull appears to be very low, an illusion caused by the crushing that it has undergone. By measuring the maxilla below the anterior horn cores, I have estimated the crushing to be about 17 per cent., so that when the skull is restored to its orignial height it is seen to be quite comparable to the skull of *Palaeotragus*. The basicranial axis forms a slight angle with the palatal surface.

The maxilla is heavy, with a slight swelling above the first and second molars, and the malar runs far forward on this bone. The latter forms the entire lower border of the orbit. The lacrymal is large, a

[1]Lankester, E. Ray. 1907. 'The Origin of the Lateral Horns of the Giraffe in Foetal Life on the Area of the Parietal Bones.' Proc. Zool. Soc. London, pp. 100–115.
1907. 'The Existence of Rudimentary Antlers in the Okapi.' Proc. Zool. Soc. London, pp. 126–135.

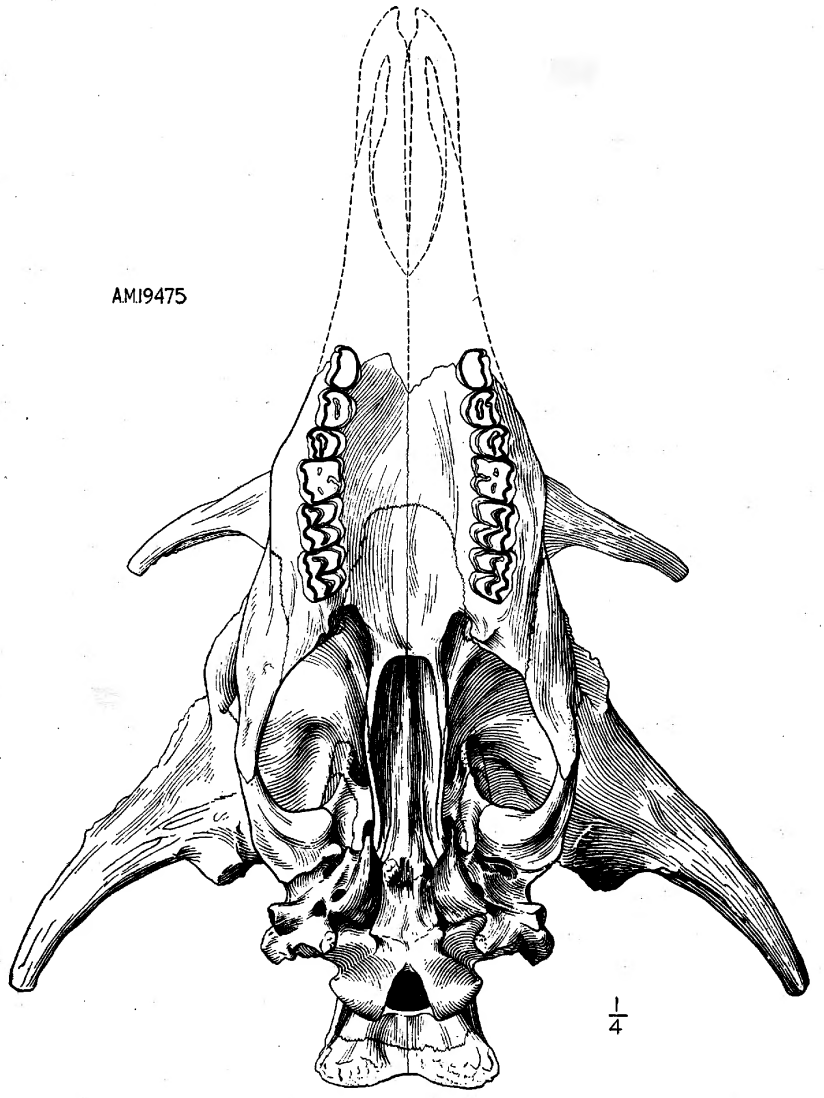

Fig. 3.—*Giraffokeryx punjabiensis* Pilgrim. Amer. Mus. No. 19475. Skull, palatal view. Muzzle restored. One-fourth natural size.

portion of it being within the orbit, and a larger portion extending forward on the side of the face. Where the lacrymal, malar and jugal meet there is a large preorbital vacuity, a characteristic feature of the giraffids. It would appear as if the trigeminus nerve traversed a maxillary sinus cavity, as in the recent giraffes.

The orbit is large, and is closed by a postorbital bar. Behind the orbit the large base of the posterior horn core projects out and back, so that it forms a heavy shelf or roof over the temporal fossa. The zygomatic arch is relatively small, and it is overhung by the base of the horn core.

Behind the glenoid is an expansion of the squamosal, carrying the tube of the external auditory meatus, and a ridge connects this expanded bone with the lambdoidal crest. Below the external auditory meatus is the paroccipital process, a fairly short but heavy structure. The occipital condyles are quite large, which would indicate that the cervical vertebrae were heavy. The supraoccipital is constricted above the foramen magnum, but it flares widely at the lambdoidal crest. The pits in the supraoccipital for the attachment of the semispinalis capitis muscle are shallow, as is characteristic of the Palaeotragine group of giraffids, as contrasted with the more advanced Sivatherines and Giraffines, in which these pits are quite deep.

In a consideration of the basicranium it may be well to take up the several elements separately, in order that they may be discussed according to their positions and functions. Therefore, the floor of the brain case will first be considered, after which there will be a discussion of the auditory apparatus, and then finally some attention will be paid to the articulations and the attachments for the jaw and for the masticating muscles.

The basicranium is rather wide in comparison to its length. The basioccipital is broad and is characterized by its large basilar tubercles, for the attachments of the rectus capitis ventralis major muscles. These tuberosities are much more prominent than in the modern okapi or giraffe; indeed, they are relatively larger than in *Samotherium* or *Palaeotragus*, and are quite comparable to the same structures in *Bramatherium*. The basisphenoid has low ridges along either edge.

In contradistinction to most of the Giraffidae, the posterior nasal choanae are situated somewhat behind the third molar, instead of being directly in line with the posterior border of the last tooth. The pterygoids of *Giraffokeryx* are developed much as they are in the okapi. Owing to the fact that this animal was fully adult, the sutures are largely

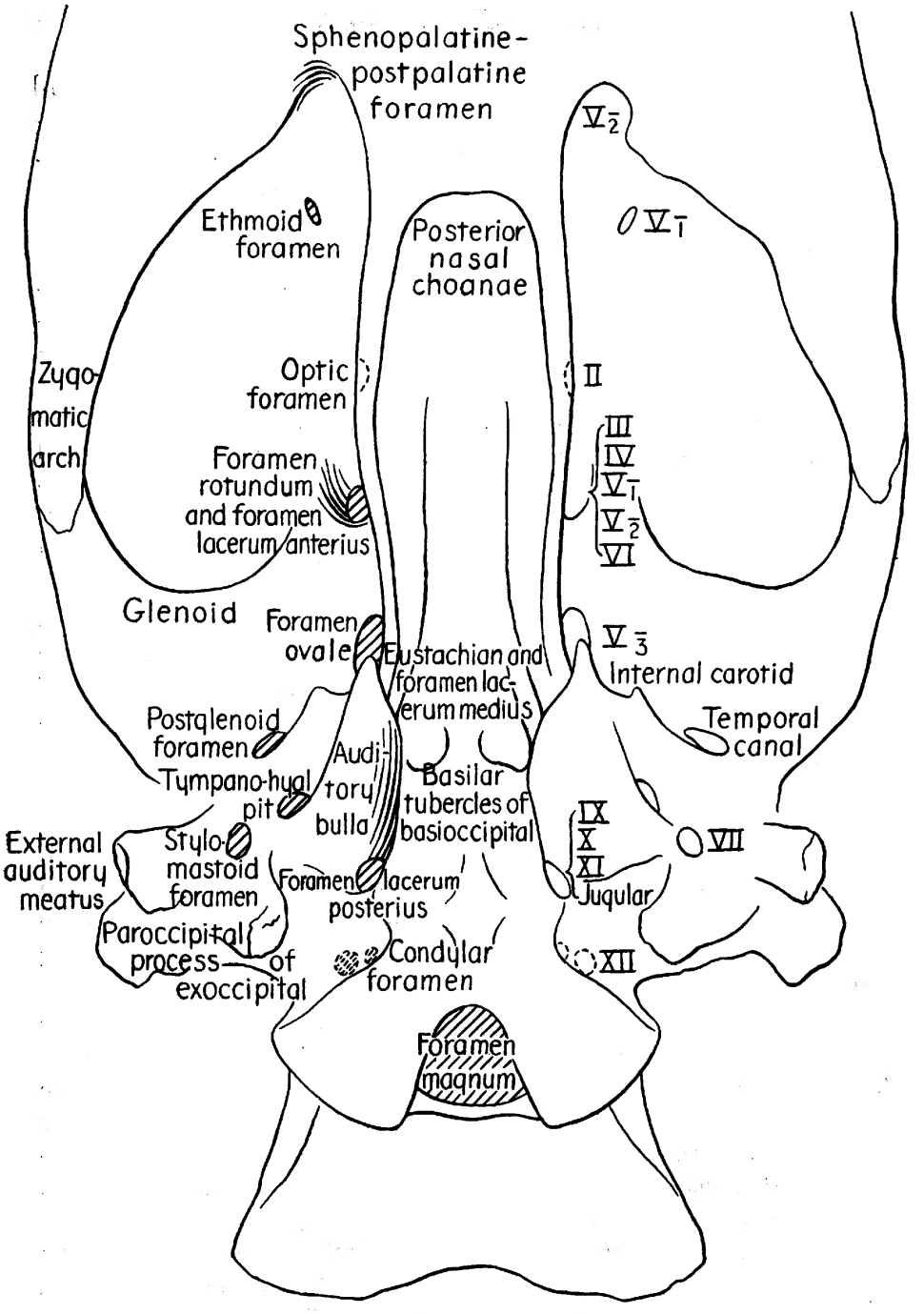

Fig. 4.—Diagram of basicranium and adjacent regions of the skull of *Giraffokeryx punjabiensis* Pilgrim. Names of foramina shown on left side of diagram; position of nerves and blood vessels on right.

obliterated, making precise determinations of the basicranial elements uncertain, but undoubtedly the alisphenoid ran well up within the orbit.

Coming now to the basicranial foramina, it may be seen that the ethmoid and optic foramina are large and separated from each other. As in the okapi there are two large foramina at the base of the alisphenoid, the anterior one of which would seem to be a fusion of the foramen rotundum and the foramen lacerum anterius, while the one posterior to it is undoubtedly the foramen ovale. Thus the anterior foramen served as a common passage for the oculomotor, the trochlear, the first and second branches of the trigeminus and the abducens nerves, while the posterior foramen transmitted the mandibular or third branch of the trigeminus. The development of the foramen lacerum medius is similar to that in the okapi, namely, it together with the opening for the Eustachian tube, is concealed above the anterior point of the bulla. The stylomastoid foramen is large, evidently carrying a well developed facialis nerve, and again, the postglenoid foramen is of unusually great size. In both of these characters, *Giraffokeryx* is similar to the okapi. The foramen lacerum posterius is of normal development, and separate from the foramen lacerum medius.

In *Okapia* there are two well developed condylar foramina for the branches of the hypoglossal nerve. It is difficult to be certain about this region in the skull of *Giraffokeryx*, because of the manner of preservation, but probably these foramina were well developed. The reader is referred to the accompanying figure of the basicranium of *Giraffokeryx*, in which the various foramina are labeled.

The auditory bulla is of medium size, though not as large nor as inflated as in *Okapia*. In *Giraffokeryx* the bony tube of the external auditory meatus points posteriorly, while in *Okapia* this structure is placed almost transversely.

Coming now to the articulation of the lower jaw, we see that the glenoids are convex as in the okapi. The pterygoids are fairly heavy, showing the power of the internal pterygoid muscles to move the jaw from side to side. The short heavy paroccipital processes would point to strong digrasticus muscles.

The palate is wide and flat. The cheek teeth are well worn, again an indication that this was a fully adult animal at the time of its death. There are but three premolars, the first one having been lost during the course of evolutionary development. The muzzle is missing anterior to P^2, but undoubtedly there was no canine, and the premaxillaries were edentulous. The cheek teeth are brachyodont, showing this animal to be

primitive, even though aberrant, and they are marked by the characteristic giraffid rugose enamel. The second and third premolars are greater in length than in width, and each tooth is characterized by a strong anterior style, and an internal posterior swelling. In the last premolar the width considerably exceeds the length. The molars are approximately quadrate, with the protocone and metaconule of about equal size, and with strong parastyles and mesostyles.

An isolated tooth (Amer. Mus. No. 19611) shows the character of the last premolar. In this tooth the median outer barrel is well developed and there is a swelling on the posterior border of the inner crescent, which when worn forms a small enamel lake within the dentine.

Amer. Mus. No. 19472, listed above, demonstrates the form of the molars much more clearly than do the teeth in the skull. In each molar, along the ectoloph, the parastyle and mesostyle are strongly developed; the anterior barrel is strong, but on the posterior part the ectoloph is flat. A similar condition holds in *Palaeotragus*, but it is to be noted that the styles and barrels in *Giraffokeryx* are divergent, while in *Palaeotragus* they are parallel, a fact that finds its explanation in the greater hypsodonty, and consequently the more advanced state of the teeth, in the latter genus. The anterior inner crescent of each molar in *Giraffokeryx* has a slight cingulum. Moreover, this crescent extends lingually further than does the posterior crescent, which gives the anterior half of the tooth a greater transverse measurement than the posterior moiety. There are no inner pillars on the molars as in *Palaeotragus*.

Pilgrim speaks of the absence of an enamel fold in the posterior crescent of the molar of *Giraffokeryx*. Such a fold is present to a greater or lesser extent in all of the American Museum specimens, and in some of them it forms an enamel loop within the dentine.

All in all, the upper teeth of *Giraffokeryx* are very similar to those of *Palaeotragus*, demonstrating (as has been pointed out above, in connection with certain cranial characters) the close relationship existing between these two genera.

THE MANDIBLE

Amer. Mus. No. 19587, listed above, contains a complete set of grinding teeth, which differ from the teeth of *Palaeotragus* and *Okapia* mainly by virtue of their relative narrowness. The second premolar is relatively simple, consisting of a median cone or point, from which a single ridge extends forward, and to the back of which there is a posterior ridge, dividing to form a Y. The third premolar is more advanced,

having the main cusp placed exteriorly. Anteriorly the ridge divides so as to form two prongs pointing lingually, while posteriorly there are three such prongs. There is a low internal wall to this tooth. In the fourth premolar the internal wall has developed to form a high internal ridge, rising to a point opposite the external cone. The external ridge divides into three prongs posteriorly, as in the preceding tooth. In P_3 and P_4 there are anterior external cingula.

The molars consist of the familiar artiodactyl crescents, and naturally in the third molar there is an additional posterior loop or talonid. Cingula are present anteriorly on the internal and external sides. The enamel is

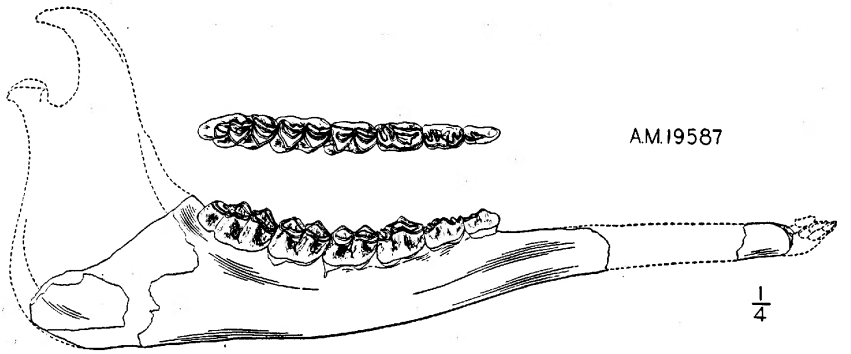

Fig. 5.—*Giraffokeryx punjabiensis* Pilgrim. Amer. Mus. No. 19587. Right ramus of mandible, lateral view. Crown view of grinding teeth, above. Restored portions indicated by dotted lines. The length of the restored premolar-canine diastema is based on comparisons with *Palaeotragus*. One-fourth natural size.

rugose. There is a strong external median pillar in the first molar, and rudimentary knobs in the succeeding teeth.

The incisor alveoli are present, but a portion of the ramus forming the diastema was lost. Undoubtedly this diastema was long, as in *Palaeotragus* or *Okapia*, and it would seem as if the ascending ramus was shaped much as in the latter genus.

MEASUREMENTS

SKULL.—Amer. Mus. No. 19475.

Length, P^2 to condyle	326 mm.
Estimated total length	500
Height above M^3 (to superior border of orbit)	85
Restored height	110
Antero-posterior diameter of orbit	66
Postorbital length (front of orbit to condyle)	222

MEASUREMENTS (*Continued*)

SKULL.—Amer. Mus. No. 19475 (*Continued*)

Estimated preorbital length	278
Width between tips of anterior horn cores	277
Width between tips of posterior horn cores	403
Width of confluent base of anterior horn cores	142
Distance between bases of posterior horn cores	123
Greatest width across squamosals	144
Width at narrowest portion of parietals	56
Width across zygomatic arches	179
Width of maxillae above P^2	80
Width of palate at M^3	66
Width of occipital condyles	76
Distance, anterior border of foramen magnum to border of posterior nasal choanae	150
Width between orbits	134
Width between tips of paroccipital processes	88

MANDIBLE.—Amer. Mus. No. 19587

Depth of ramus below third molar	43

UPPER DENTITION.—

	Giraffokeryx punjabiensis Amer. Mus. No. 19475		*Palaeotragus microdon* (After Bohlin)[1]	
	Antero-posterior	Transverse	Antero-posterior	Transverse
P^2	22 mm.	19 mm.	18 mm.	mm.
P^3	20.5	20	18	20
P^4	17.5	21	18	23
M^1	22	24	23	27
M^2	25	27	26	30
M^3	24.5	26	25	27

LOWER DENTITION.—

	Amer. Mus. No. 19587		(After Bohlin)[2]	
P_2	18	9	—	10
P_3	20.5	12	15	13
P_4	24	15	18	15
M_1	24	16	—	17
M_2	25	27	23	18
M_3	37	17	36	18

Ratio, premolar to molar length

Upper dentition	83	73
Lower dentition	71	55[3]

[1]Bohlin, B. 1927. 'Die Familie Giraffidae.' Pal. Sinica, Ser. C, IV, Fas. i, p. 27, column d in table.

[2]Bohlin, B. 1927. *op. cit.*, p. 29, column I in table.

[3]Missing measurements obtained from other specimens listed by Bohlin.

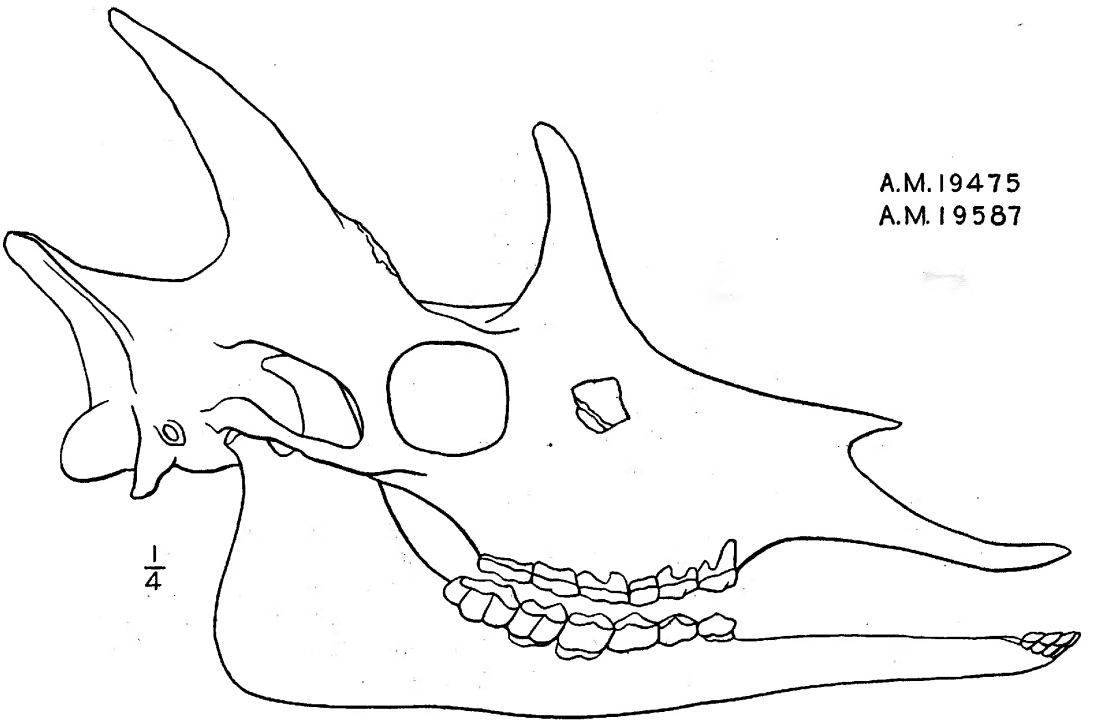

Fig. 6.—Restoration of the skull and mandible of *Giraffokeryx punjabiensis* Pilgrim, showing the probable appearance of the skull with the crushing removed. One-fourth natural size.

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